

Social Behaviours in Solitary Bees: Interactions Among Individuals in *Xeralictus bicuspidariae* Snelling (Hymenoptera: Halictidae: Rophitinae)

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Abstract.—Understanding behavioural interactions among ancestrally solitary species is key to understanding the evolutionary origins of group living and cooperation. Previously, Packer (2006) showed that circle tube arenas can be used to evaluate the social status of species for which nesting data are unavailable. We used circle tube arenas to study the behaviour among 30 female dyads of the solitary halictid bee, *Xeralictus bicuspidariae* Snelling, a member of the subfamily Rophitinae, all members of which are ancestrally solitary. Overall, 75.2% of frontal encounters resulted in avoidance, 20.7% in aggression, and 4.1% in a successful pass, values which are similar to those previously observed in solitary halictids. Although passing events, which are interpreted as cooperative behaviour, were rare, they were significantly correlated with bees' rates of approach and avoidance, and also with differences between dyad members in rates of ovarian development. Rates of aggression were not correlated with physical traits of females or with other behaviours. We compare the circle tube behaviour of *X. bicuspidariae* to previously studied solitary and social halictids, and provide statistical support for this method of assessing social status.

The origin of eusociality is one of the major events in the evolutionary history of life (Szathmáry and Maynard Smith 1995), yet our understanding of what transpires during transitions to sociality remains poor. One reason is the great age at which most solitary to eusocial transitions took place – over 100 million years ago for termites, ants, and vespid wasps (Wenzel 1990; Martinez-Delclos and Martinell 1995), perhaps somewhat less in the bees (Michener and Grimaldi 1988), and around 20 million years ago in the three main lineages of eusocial Halictinae (Brady et al. 2006). The great age of these social lineages means that to investigate the evolutionary origins of sociality, we must often use comparative methods based on detailed knowledge of the behaviour of extant species. However, a second reason for our incomplete understanding of the origins of

eusociality stems from our poor knowledge of solitary species, whose behaviour is most likely to represent the ancestral forms from which sociality evolved.

Sweat bees (Halictidae: Halictini and Augochlorini) are the most socially variable group of animals on earth, including species that run the gamut from obligately solitary to obligately social, with sociality varying from communal to semisocial and eusocial forms (Schwarz et al. 2007). There are even examples of intraspecific social polymorphism, in which solitary or social behaviour is expressed within or among populations, often in response to variability in environmental conditions (Schwarz et al. 2007). The ecological processes that shape the social behaviour of modern halictines are often considered to be analogous to those that shaped the evolution of major social transitions in the subfamily as a whole, including at least three origins of eusociality and multiple reversions to

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solitary behaviour (Danforth et al. 2003; Danforth et al. 2008).

Recent behavioural studies provide intriguing evidence that behavioural transitions from solitary to social behaviour may occur easily and rapidly. Jeanson et al. (2005) observed that in forced associations of solitary *L. (Chilalictus) NDA-1* or of communal *L. hemichalceum*, both dominance interactions and division of labour arose as natural outcomes of normal solitary behavioural patterns expressed in the context of novel, social environments, the effect being stronger in the solitary than in the communal species. A similar phenomenon occurred in experiments on solitary *Ceratina* carpenter bees (Apidae, Xylocopinae) when females were forced to nest in social associations (Sakagami and Maeta 1977). This suggests that at the very beginning of evolutionary transitions to caste-based sociality, 'emergent' social behaviour by solitary bees could provide the behavioural substrate upon which natural selection acts, before the evolution of caste-based sociality. This fascinating possibility makes understanding the behaviour of obligately solitary bees all the more critical.

Although behavioural interactions among individuals of social and socially polymorphic sweat bees have been studied in detail on numerous occasions (Breed et al. 1978; Buckle 1984; McConnell-Garner and Kukuk 1997; Wcislo 1997; Soucy 2002), solitary species have received less attention. Consequently, we know little about the potential for social interactions among individuals of solitarily nesting species, and how naturally occurring variation in individual behaviour might impinge upon the development of sociality remains obscure. Of course, one problem with studying the behaviour of solitary bees is a dearth of opportunities for observing known individuals under natural conditions at sufficient frequency to permit detailed analysis. Fortunately, a recent comparative study suggests that the circle tube arena, a circle of clear plastic tubing in which bees are

forced to interact (Breed et al. 1978), is one route to obtain sufficient behavioural data on interactions among individuals of solitary species (Packer 2006).

In this paper we analyse the results of a detailed study of interactions among individuals in a solitary species of the bee family Halictidae. *Xeralictus bicuspidariae* Snelling is a member of the halictid subfamily Rophitinae with several advantages as a study organism. First, the phylogenetic position of rophitine bees suggests that their solitary behaviour is ancestral, i.e. there is no evidence that there has been any sociality in the evolutionary history of the entire subfamily (Danforth et al. 2008; Patiny et al. 2008), so any potential for social interactions that might be induced experimentally, is part of its solitary ground plan. Second, this bee exhibits considerable variation in colour of the metasoma of females (Snelling and Stage 1995) such that pairs can easily be chosen to permit individual recognition without the intervention of artificially marking the bees (marking has been shown to influence interactions among individuals; Packer 2005). Third, it is a large bee, facilitating observations of behaviours.

METHODS

Xeralictus bicuspidariae was studied at Dome Rock Road, La Paz County, Arizona, USA, in April 2005. Female bees were collected from flowers of *Mentzelia* (Loasaceae) and retained in microcentrifuge tubes for no more than 30 minutes before behavioural observations commenced. This duration between capture and observation was maintained to reduce the effect of captivity-induced physiological changes upon behaviour (Pabalan et al. 2000). Two bees were then placed simultaneously in a clean, plastic circle tube of internal diameter 7 mm and length 20 cm. Simultaneous entry precludes ownership effects (Wcislo 1997), and this tube diameter was sufficient for the two individuals to pass one another and to turn around (Packer 2005), but

narrow enough that one bee could block an attempted pass by the other. Observations lasted for fifteen minutes, a time period sufficient for differences in behaviour between individuals within a pair to be detected, and took place outdoors in the shade. The metasomal colour of females varied from entirely brick red to entirely dark brown (Snelling and Stage 1995); pairs were set up with one red and one dark female that could be easily differentiated by the observer without being artificially marked. Several experiments were terminated when discrimination between the individuals was found to be more difficult than expected.

An approach was taken to have occurred when individuals came within a distance of one body length of each other (Kukuk 1992; Packer 2005). Both frontal (head to head) and front-to-back (head to tail) encounters were assessed and their outcomes classified into categories: approaches, aggression, avoidance and passes. Aggressive interactions included nudges, lunges and C-postures. Interactions that resulted in avoidance arose when one individual moved away from a stationary individual or they both moved away from each other. A pass was scored when the two bees manoeuvred to permit one to move past the other, or they both moved past one another simultaneously. All behavioural observations were carried out by LP, and are therefore directly comparable to the data presented in Packer (2006). For more detailed descriptions of individual behaviours, see Batra (1966).

All bees were measured and assessed for relative age and reproductive condition as follows. Head width was measured as the greatest distance across the compound eyes; this was the greatest diameter of the head in dorsal view. Relative wear was assessed from mandibles, scored from 0 (unworn) to 6 (worn to the base of the subapical mandibular tooth), and from wings (the total number of nicks along the margin of the left forewing).

Reproductive status was estimated based upon dissection of the metasoma. The spermatheca was inspected for the presence of sperm and ovarian development was assessed by estimating the size of oocytes in each ovariole relative to the size of a fully developed oocyte, and summing the resulting proportions across all six ovarioles. As expected for a solitary bee during nest provisioning, all females had mated and so matedness was not considered further.

Statistical analysis.—In circle tubes, the behaviour of each member of a pair is affected by the behaviour of the second member of the pair. This creates a problem of statistical non-independence between members of each dyad. A second problem is variation in behavioural rates among pairs – some pairs are very active and some do almost nothing. A common approach has been to standardize focal behaviors by the encounter rate, which in effect means all the behaviours are analyzed as ratios, so information related to absolute frequency is lost and the statistical problems of analysing ratios are gained. To address these issues, we present an approach somewhat different than in previous circle tube studies. First, when behavioural patterns of individuals are considered, we analyse only one individual per dyad (red bees or dark bees), which avoids inflating the number of degrees of freedom in each measurement. Second, when properties of dyads are considered, we analyse both behavioural frequencies and physical traits in terms of differences between each bee in a pair. Correlations between trait differences can be interpreted in the same way as correlations between the traits themselves. For instance, a negative correlation between head width difference and wear difference would indicate that larger bees tended to be less worn. All differences between pair members were calculated as (value for red bee) – (value for dark bee), except for head width (HW) difference, which was calculated as (red HW – dark HW) / average HW.

Table 1. Physical characteristics of adult female *Xeralictus bicuspidariae* used in circle tube experiments. Signed rank tests were used to compare the physical characteristics of red and dark females in each dyad; non-significant (n.s.) results indicate that overall, red and dark females were equivalent.

Variable	Mean	SD	Range	Signed rank test
Head width (mm) (n=56)	7.4	0.24	7.0–8.0	S = -22.5, n.s.
Mandibular wear (n=56)	2.1	1.2	0–5	S = 31.5, n.s.
Wing wear (n=48)	8.0	5.1	0–20	S = 4.0, n.s.
Total ovarian score (n=55)	1.7	0.4	0.5–2.6	S = 8.0, n.s.

All variables, including differences, were checked for normality using the array of tests in SAS 9.1 (PROC UNIVARIATE); since several variables were non-normally distributed, we mainly used non-parametric statistical methods. Additionally we used principal components analysis (PCA) to further explore and confirm relationships among physical and behavioural variables in *X. bicuspidariae*. Initially, the PCA was based on eight variables (entered as untransformed differences between females in mandibular wear, wing wear, head width, total ovarian score, approach frequency, aggressive frequency, avoidance frequency, and pass frequency). However, since Kaiser's Measure of Sampling Adequacy (MSA) with all eight variables had a value of only 0.467, the variable with the lowest communality measure (head width) was dropped from the PCA. With the remaining seven variables, MSA=0.63, which exceeds the 0.6 criterion. We present both factor loading scores (the degree to which each variable influences the inferred factors) and communality estimates (a reliability score which estimates the proportion of variance in each variable that is jointly explained by all three factors).

Packer (2006) argued that the social status of halictine bees can be accurately assessed using circle tube assays of females, even in the absence of nesting data. Solitary bees should be characterized by high levels of avoidance behaviour, communal bees by high levels of cooperative behaviour (passing) and low levels of aggression, and semisocial and eusocial

bees by low levels of cooperation and high levels of both aggression and avoidance. We used discriminant functions analysis (DFA) to assess how accurately *X. bicuspidariae* and 21 other species (references in Packer 2006) can be categorized as solitary, communal, or semi and eusocial, based on the percentages of avoidance, aggression, and passing behaviours in circle tubes.

RESULTS

Circle tube assays.—Physical traits of the 60 females used in 30 circle tube trials are presented in Table 1. There were no significant correlations among body size, degree of wear, and degree of ovarian development within individuals used in the behavioural tests, although degree of mandibular wear was positively correlated with degree of wing wear (Pearson correlation coefficient, $r=0.55$, $n=48$, $p<0.0001$). All females had at least one $\frac{1}{4}$ -size, developing oocyte, and 25 of 52 (48%) dissected females contained a full-size oocyte, ready to lay. The mean difference between red and dark females in each dyad for each of these characteristics, was zero (Table 1), so bee colouration had no significance other than providing a convenient identification tool for the observer.

The frequencies of each of the four classes of behaviour per dyad and per female are given in Table 2. The most frequent behaviours were approaches (32.5 per dyad) and avoidance (25.1 per dyad), followed by aggressive behaviours (6.7 per dyad) and passing (1.2 per dyad).

Table 2. Behavioural frequencies for approach, avoid, pass, and aggressive behaviours. Note that 'aggression' includes C-postures, biting, and pushing. Since the behavioural rates of each member of a dyad are non-independent, only one bee per dyad is used to provide an estimate of behavioural frequencies per individual. Measurements of mutual behaviour refer to simultaneous performance of that behaviour by both members of a dyad. Sample size N=30 dyads, except where otherwise noted.

Behaviour	Rate	Mean	SD	Range
Frontal encounters	Dyad total	33.0	8.3	13–46
Approach	Dyad total ¹	32.5	9.1	11–52
	Red female ¹	4.6	4.8	0–22
	Dark female	7.6	7.4	0–35
	Mutual	20.3	10.6	0–44
Avoid	Dyad total	25.1	7.5	10–37
	Red female	9.3	4.3	3–19
	Dark female	9.7	4.3	0–20
	Mutual	6.1	4.0	0–13
Pass	Dyad total	1.2	1.1	0–4
	Red female	0.3	0.5	0–2
	Dark female	0.2	0.6	0–3
	Mutual	0.7	0.9	0–3
Aggression	Dyad total	6.7	5.0	1–19
	Red female	3.8	3.8	0–16
	Dark female	2.9	3.0	0–11

¹N=29

Overall, 75.2% of frontal encounters resulted in avoidance, 20.7% in aggression, and 4.1% in a successful pass.

Aggressive acts were observed in all 30 pairs, and by 52 of the 60 (87%) individuals assayed. Withdrawals were also observed in all 30 pairs; only 1 bee of 60 (2%) did not display a unilateral withdrawal, but she did take part in a mutual (bilateral) withdrawal. Passing or cooperative acts were rare, being observed in only 22 of 30 (73%) pairs. Of a total of 35 passes, 20 (57%) were bilateral (both bees moved past each other) and 15 (43%) were unilateral (1 bee moved past the other bee).

Based on behavioural frequency differences (red bee – dark bee), three behaviours, approach, avoid, and pass were found to be mutually positively correlated (i.e. the bee that did one behaviour more frequently also did the other behaviour more frequently; Spearman rank correlations: approach vs. avoid, $r=0.798$, $n=29$, $p<0.0001$, approach vs. pass: $r=0.577$, $n=29$, $p=0.001$; avoid vs. pass: $r=0.460$, $n=30$, $p=0.010$), but none was correlated with the frequency of aggression (aggress

vs. approach: $r=-0.224$, $n=29$, n.s.; aggress vs. pass: $r=-0.106$, $n=30$, n.s.; aggress vs. avoid: $r=-0.193$, $n=30$, n.s.).

Differences between bees with respect to head width, wing wear, and mandibular wear were not significantly correlated with differences in behavioural frequency for any of the behaviours. Differences in total ovarian score did correlate positively with the rates of approach and pass, although not with either avoidance or aggressive frequencies (Table 3, Fig. 1). In other words, the female with greater ovarian development was almost significantly likely to approach and was significantly more likely to pass than the female with lesser ovarian development.

A principal components analysis (PCA) further describes behavioural and physical variation among female interactants in circle tubes. As outlined in the Methods, the PCA (Table 4) included all variables except head width, which contributed little to understanding variation among the dyads. Three factors had eigenvalues > 1.0 and were retained, explaining 77.9% of the variation among dyads. Factor 1 was

Table 3. Influence of female physical status on behaviour. Spearman rank correlations were based on differences in both female traits and differences in behaviour frequencies (red bee – dark bee). Positive correlations indicate that the bee with the greater trait value exhibited the behaviour more frequently.

Physical trait of females	Behaviour (N=number of dyads)			
	Approach	Avoid	Cooperate	Aggression
Head width	0.197 (27)	0.018 (28)	-0.054 (28)	0.292 (28)
Wing wear	0.020 (20)	-0.123 (21)	-0.092 (21)	0.077 (21)
Mandibular wear	-0.007 (27)	-0.100 (28)	-0.068 (28)	0.215 (28)
Total ovarian score	0.451 (26), p=0.062	0.250 (27)	0.435 (27), p=0.023	-0.132 (27)

most influenced by non-aggressive behaviour and ovarian development, reflecting the previously noted positive association between ovarian development and approach and passing frequencies. Factor 2 was influenced mainly by mandibular and wing wear; thus Factor 2 describes varia-

bility in wear differences among dyads, and so does not reflect behavioural variation. Factor 3 was influenced mainly by aggression. PCA based only on the four behavioural frequency differences, resulted in two factors that together explained 79.7% of the variation among

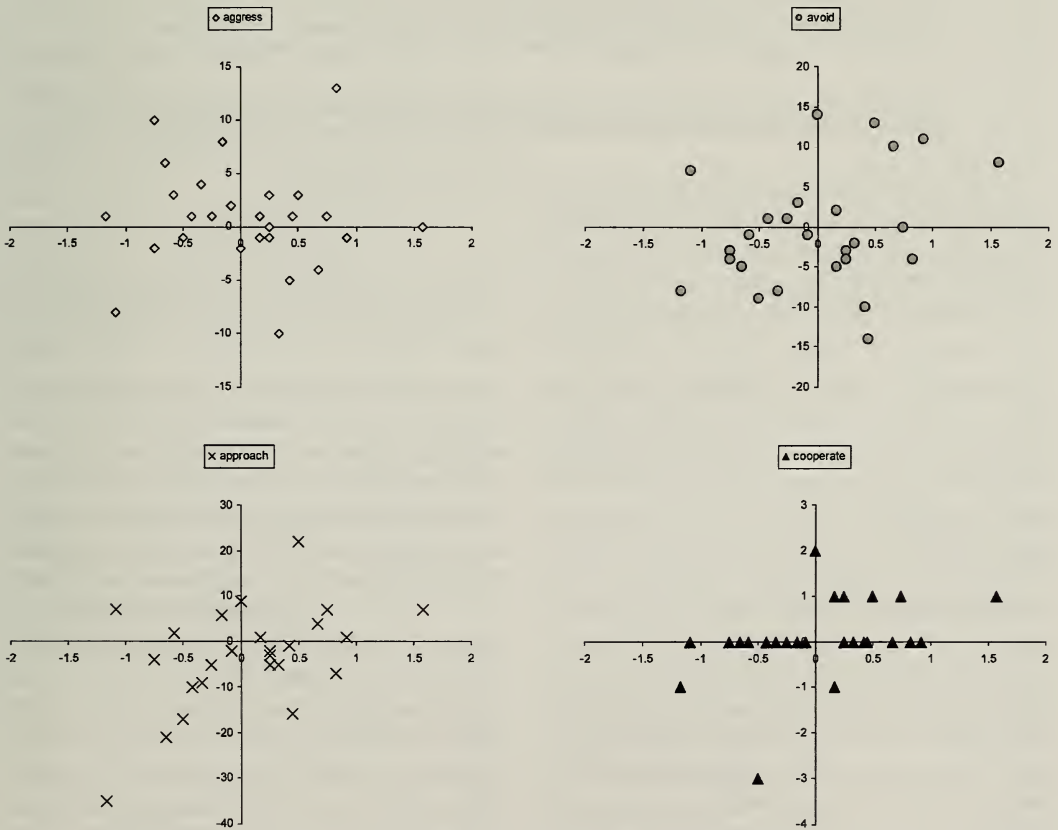


Fig. 1. Influence of ovarian development (OD, horizontal axes) on different behaviours (vertical axes), scored in terms of the differences between individuals (red-dark). Positive values on the horizontal and vertical axes indicate a greater value for the red bee, whereas negative values indicate a greater value for the dark bee. Top left: OD vs. aggression. Top right: OD vs. avoidance. Bottom left: OD vs. approach frequency. Bottom right: OD vs. cooperation (pass).

Table 4. Principal components analysis describing variation among dyads based on differences between interactants in both physical and behavioural traits. Three factors were retained with eigenvalues > 1 , explaining a cumulative total of 77.9% of the variation among dyads. Relatively strong factor loading scores (>0.6) are indicated in boldface. Community estimates describe the proportion of variance in each trait that is jointly explained by Factors 1, 2 and 3. Kaiser's overall Measure of Sampling Adequacy (MSA) was 0.6312.

Trait (difference between females)	Factor 1	Factor 2	Factor 3	Communality estimate
Mandibular wear	0.0124	0.9064	-0.0567	0.4962
Wing wear	-0.1391	0.7738	-0.5193	0.4465
Ovarian score	0.6217	0.3534	0.2441	0.7520
Approaches	0.9017	0.0752	-0.1593	0.6582
Avoidance	0.8311	-0.0742	-0.2158	0.7008
Pass	0.8116	-0.0438	0.2910	0.7450
Aggression	-0.1848	0.5085	0.7388	0.5381
Eigenvalue	2.602	1.817	1.035	
Variance explained	37.2%	26.0%	14.8%	

dyads. Factor 1, which explained 55.0% of the behavioural variation among dyads, was strongly influenced by approaches (loading score 0.910), avoidance (0.866), and passes (0.752). Factor 2, which explained 24.6% of the variation, was strongly influenced by aggression (loading score 0.959).

Comparison of X. bicuspidariae with other halictines.—Fig. 2 compares *X. bicuspidariae* to 21 other species, in terms of the proportion of avoidance, aggressive, and cooperative (passing) behaviours observed in circle tube assays. It most closely resembles *Penapis toroi*, another solitary rophitine. Discriminant functions analysis (DFA) based on four putative categories (solitary, communal, semisocial, and eusocial) perfectly assigned solitary and communal species, but failed to distinguish between the latter two, assigning 1 eusocial species to the semisocial category and 1 semisocial species to the eusocial category. DFA based on three putative categories (solitary, communal, and caste-based social) reassigned each species into the category presented in Fig. 2. Moreover, when *Caenohalictus pygostinuatum* was categorized as communal (Michener et al. 1979), then DFA assigned it to the solitary group (as suggested by Packer 2006). The success of the DFA approach is based on significant differences among solitary, communal, and

caste-based social bees in the proportions of aggressive behaviour (ANOVA, $F=50.32$, $df=2,19$, $p<0.0001$) and avoidance behaviour (ANOVA, $F=15.15$, $df=2,19$, $p<0.0001$), as well as significantly more frequent passing behaviour in communal species, as compared to both solitary and social species (ANOVA, $F=62.55$, $df=2,19$, $p<0.0001$).

DISCUSSION

Solitary behaviour of X. bicuspidariae.—In *X. bicuspidariae*, differences between circle tube interactants in head width, wing wear, and mandibular wear were not associated with differences in behaviour, suggesting that neither body size nor wear (and possibly age) structured interactions among adult females. Differences in ovarian development (OD) also did not predict differences in either aggression or avoidance, but were associated with rates of approach and pass behaviours, these being exhibited more frequently by the bee with greater ovarian development. Why would high OD females be more likely to approach and especially, to pass? One possibility is that the closer a female is to laying an egg, the more active she is likely to be. Under natural circumstances, a female halictine getting ready to lay an egg should be spending considerable time readying a brood cell and provisioning it. In a circle

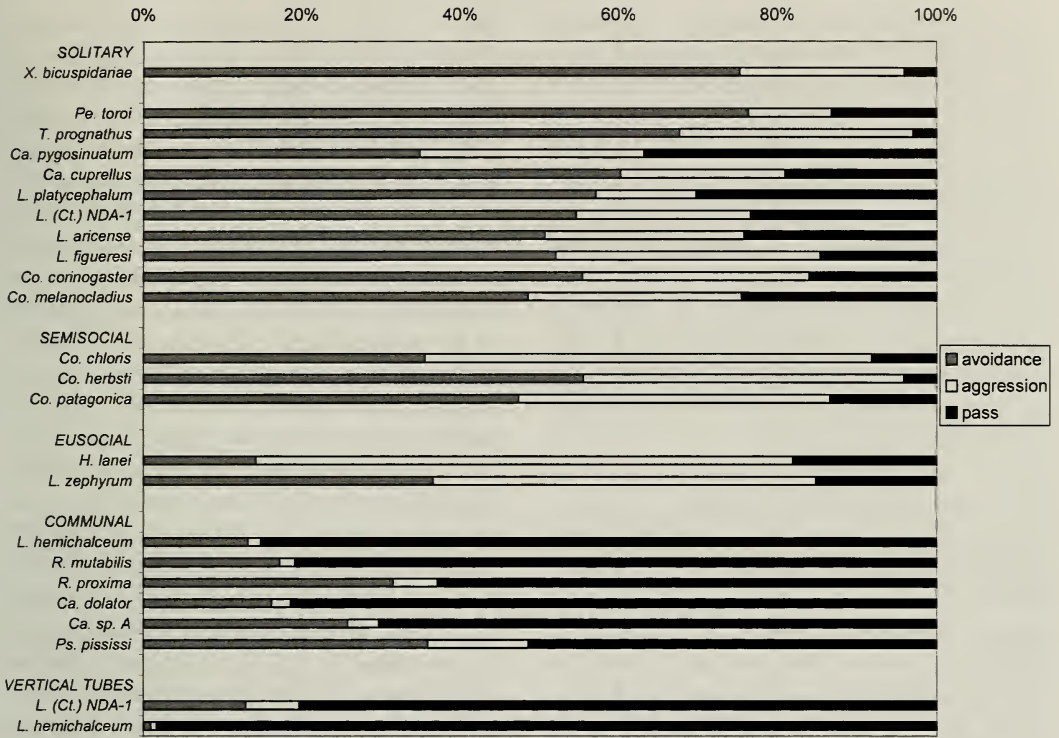


Fig. 2. Comparison of circle tube behaviour of *X. bicuspidariae* with literature values (partially redrawn from Packer 2006, which also contains a complete list of references). Solitary bee species are characterized by high rates of avoidance (withdrawals), communal bees by high rates of cooperation or tolerance (passing), and semisocial and eusocial species by high rates of aggression, coupled with very low rates of passing. Differences in behavioural profiles of bees tested in circle tubes versus vertical tubes (Jeanson et al. 2005) are evident. Genera represented (top to bottom) are *Xeralictus* (*X.*), *Penapis* (*Pe.*), *Thrincohalictus* (*T.*), *Caenohalictus* (*Ca.*), *Lasioglossum* (*L.*), *Corynura* (*Co.*), *Halictus* (*H.*), *Ruizantheda* (*R.*), and *Pseudagapostemon* (*Ps.*).

tube, heightened activity rates make it more likely that a bee will approach the second bee, and then perhaps continue right past her. In other words, bees with higher ovarian development may be more motivated to remain active, which in a circle tube would result in higher rates of approaching and passing.

The lack of correlation between ovarian status and aggression might seem surprising, but is consistent with observations in other species, including the solitary halictine, *L. (Ctenonomia) NDA-1*, and the communal species, *L. (Chilalictus) platycephalum*, in which ovarian status was not associated with aggression (McConnell-Garner and Kukuk 1997). In contrast, in *Lasioglossum figueresi* the female with larger ovaries was often first to be aggressive, and

the bee with smaller ovaries was often first to withdraw (Wcislo 1997). Even in obligately eusocial species like *Halictus ligatus*, dominance, aggression, and defensive behaviours are most likely and most severe when the two members of a dyad both have relatively high ovarian development, for example, when a queen is paired with a worker with highly developed ovaries (Pabalan et al., 2000). This suggests that correlations between OD and aggression might have more to do with reactions to the threat of egg replacement than with dominance behaviour *per se*. In solitary bees, we should not then expect to see a correlation between ovarian development and aggressive behaviour (or withdrawal behaviour) except perhaps in species with high rates of intraspecific egg parasitism.

Our experiments uncovered considerable variability among individuals. Random pairings of individuals with different behavioural tendencies (personalities) must then have contributed to variation among dyads, creating behavioural scenarios that bear a marked resemblance to those expressed by social bees. Indeed, this would seem to be the basis of the phenomenon of 'emergent' sociality as described by Jeanson et al. (2005). However, the use of the term 'emergent' to describe forced social interactions among solitary bees is somewhat problematic, even in those which like *X. bicuspidariae* are ancestrally and monomorphically solitary. This is because solitary bees may also experience social interactions that insect sociobiologists do not usually categorize as 'social', such as interactions between foragers on flowers, between nest residents in dense nesting aggregations, between nest residents and would-be nest usurpers, or between residents and egg kleptoparasites. Moreover, group living may occur at very low frequencies in some solitary species without extensive nest observations, as has recently been found for several species of the apid genus, *Ceratina* (Rehan et al. 2009). In other words, many solitary bees, both ancestrally solitary and ancestrally social, may have considerable scope for intraspecific social behaviour, even if they rarely or never nest in multifemale groups. The variability in behavioural syndromes of solitary halictines (Fig. 2) suggests that eventually it may be possible to detect differences among obligately solitary, socially polymorphic, and reversed solitary species, especially based on the frequency of avoidance and aggression.

Behavioural changes in social transitions.— One caveat to the use of artificial arenas for observing bee behaviour is that the frequencies of circle tube behaviours may or may not represent the frequencies of same or similar behaviours in natural settings. Indeed, there are obvious differences in behavioural frequencies assessed using

horizontal circle tubes versus vertical linear tubes (Fig. 2), implying that major differences in behavioural frequencies are produced by different experimental methodologies. Nevertheless, the interspecific consistency of behavioural syndromes observed in circle tube assays of solitary, communal, and caste-based social species is striking and statistically supportable, suggesting that when circle tube assays are used consistently, they uncover fundamental differences in behaviour among solitary, communal, and semisocial and eusocial species. These differences, if not the behavioural frequencies themselves, can be used to infer general behavioural tendencies in bees of different social levels.

In halictids, the ancestral trait of intolerance is suggested by high rates of avoidance in solitary bees such as *X. bicuspidariae* and another solitary rophitine species, *Penapis toroi*, in which avoidance behaviours comprise about 75% of encounters (Fig. 2). Transitions to communal versus caste-based social behaviour may be quite different. Circle tube assays imply that solitary-communal transitions involve significant decreases in both aggression and avoidance, whereas transitions to caste-based eusociality involve a significant increase in aggression, coupled with a decrease in avoidance. To the extent that passes represent cooperative interactions, solitary-communal transitions would appear to involve huge increases in cooperation whereas transitions to caste-based eusociality involve little change or perhaps even a decrease in cooperative behaviour. It will be important in future studies of both solitary and social halictines, to assess the degree of behavioural concordance between natural versus artificial contexts whenever possible, so that we can actually understand how representative circle tube behaviour is for those species for which nesting data are unobtainable.

Given that one of the most outstanding features of the eusocial insects is their frequent and sophisticated cooperative

behaviour, the hypothesis that transitions to caste-based sociality should involve decreases in cooperation coupled with increases in aggression seems contradictory. However, semisocial and eusocial halictines not only interact with many more individuals than solitary bees do, but they must also cope with dominance-subordination relationships, many of which are regulated by aggressive behaviour (Kukuk and May 1991; Pabalan et al. 2000). Semisocial and eusocial bees must be able to exercise both tolerance and aggression with the same individuals. Although aggressive behaviours by solitary and caste-based social bees in circle tubes may appear to be similar, a major difference in natural settings is that aggressive behaviour by the latter is likely modulated by nest-mate recognition, such that encounters with non-nestmates will likely provoke aggression, whereas encounters with nestmates may engender aggression, tolerance, or cooperation (Peso and Richards 2010), depending on the immediate behavioural context.

Transitions to social behaviour, especially to caste-based sociality, are rarer in halictines than reversals to solitary behaviour (Danforth et al. 2003). Recent evidence suggests that reversals to solitary behaviour do not necessarily retrace the original evolutionary steps that led to sociality. For instance, reversed-solitary *Lasioglossum* have retained the social nesting characteristic of constructing brood cells close to the main burrow, facilitating both maternal inspection and care of the cells (Plateaux-Quénu 2008), and the potential for social interactions among newly emerged, adult brood. Thus reversed solitary bees may have lost caste-based sociality, but may have retained the context-dependent ability to discriminate nestmates from non-nestmates. Circle tube comparisons of ancestrally solitary species like *X. bicuspidariae*, and reversed-solitary species like *L. figueresi*, may help to illuminate and distinguish the evolutionary sequences involved in

forward and reverse social transitions, especially where these involve the expression of context-dependent behaviour.

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